PhytoKeys 229: 47–60 (2023)
DOI: 10.3897/phytokeys.229.103888

Short Communication

Malus includes *Docynia* (Maleae, Rosaceae): evidence from phylogenomics and morphology

Guang-Ning Liu[1,2*], Dai-Kun Ma[3*], Chao Xu[3], Jian Huang[4], Bin-Jie Ge[5], Qiang Luo[6], Yu Wei[1,2], Bin-Bin Liu[3]

1 *Beijing Botanical Garden, Xiangshan-Wofosi Road, Beijing 100093, China*
2 *Beijing Floriculture Engineering Technology Research Centre, Beijing, China*
3 *State Key Laboratory of Systematic and Evolutionary Botany, Institute of Botany, Chinese Academy of Sciences, No. 20. Nanxincun, Xiangshan Road, Beijing 100093, China*
4 *CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Xishuangbanna 666303, China*
5 *Eastern China Conservation Center for Wild Endangered Plant Resources, Shanghai Chenshan Botanical Garden, No.3888 Chenhua Road, Songjiang District, Shanghai 201602, China*
6 *Institute of Agricultural Sciences, Xichang College, No. 1. Xuefu Road, Anning Town, Xichang City, 615013, China*

Corresponding authors: Bin-Bin Liu (liubinbin@ibcas.ac.cn); Yu Wei (weiyu@chnbg.cn)

Abstract

Docynia has been treated as a separate genus or merged into *Cydonia* or *Docyniopsis*. Our phylogenomic evidence from 797 single-copy nuclear genes and plastomes confirmed the sister relationship between *Docynia* and *Docyniopsis*. By integrating the phylogenomic and morphological evidence, we propose to accept a broad generic concept of *Malus* and merge *Docynia* into *Malus*. Three new combinations are also made here: *Malus delavayi* (Franch.) B.B.Liu, *M. indica* (Wall.) B.B.Liu and *M. longiunguis* (Q.Luo & J.L.Liu) B.B.Liu.

Key words: *Docynia*, *Malus*, nomenclatural transfer, phylogenomics, taxonomy

OPEN ACCESS

Academic editor: Alexander Sennikov
Received: 23 March 2023
Accepted: 17 May 2023
Published: 7 July 2023

Citation: Liu G-N, Ma D-K, Xu C, Huang J, Ge B-J, Luo Q, Wei Y, Liu B-B (2023) *Malus* includes *Docynia* (Maleae, Rosaceae): evidence from phylogenomics and morphology. PhytoKeys 229: 47–60. https://doi.org/10.3897/phytokeys.229.103888

Copyright: © Guang-Ning Liu et al.
This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

Introduction

Docynia Decne. is a genus belonging to the apple subtribe Malinae and this genus is endemic to East and Southeast Asia (Yu and Ku 1974; Phipps et al. 1990; Gu and Spongberg 2003). Due to the easily distinguished multiple ovules per locule, 3-10 in *Docynia* (Fig. 1B2, B3) versus two in *Malus* Mill. (Fig. 1C2, C3), *Docynia* has been recognised as a separate genus in a series of taxonomic treatments (i.e. Decaisne (1874); Focke (1888); Koehne (1893); Rehder (1940, 1949); Yu and Ku (1974); Robertson et al. (1991); Kalkman (2004)). However, due to the multiple ovules per locule shared with *Cydonia* Mill. (Fig. 1A2, A3), Spach (1834) and Wenzig (1883) proposed an alternative taxonomic treatment, merging *Docynia* into *Cydonia*.

Recent phylogenetic and phylogenomic studies presented strong topological discordance amongst nuclear/plastid genes and showed cytonuclear conflicts (referring to fig. 1 in Liu et al. (2022)). *Docynia* is closely related to *Docyniopsis* (C.K.Schneid.) Koidz. (= *Malus* sect. *Docyniopsis* C.K.Schneid.), based on the plastomes and the nuclear sequences (Lo and Donoghue 2012; Liu et

* These authors have contributed equally to this work.

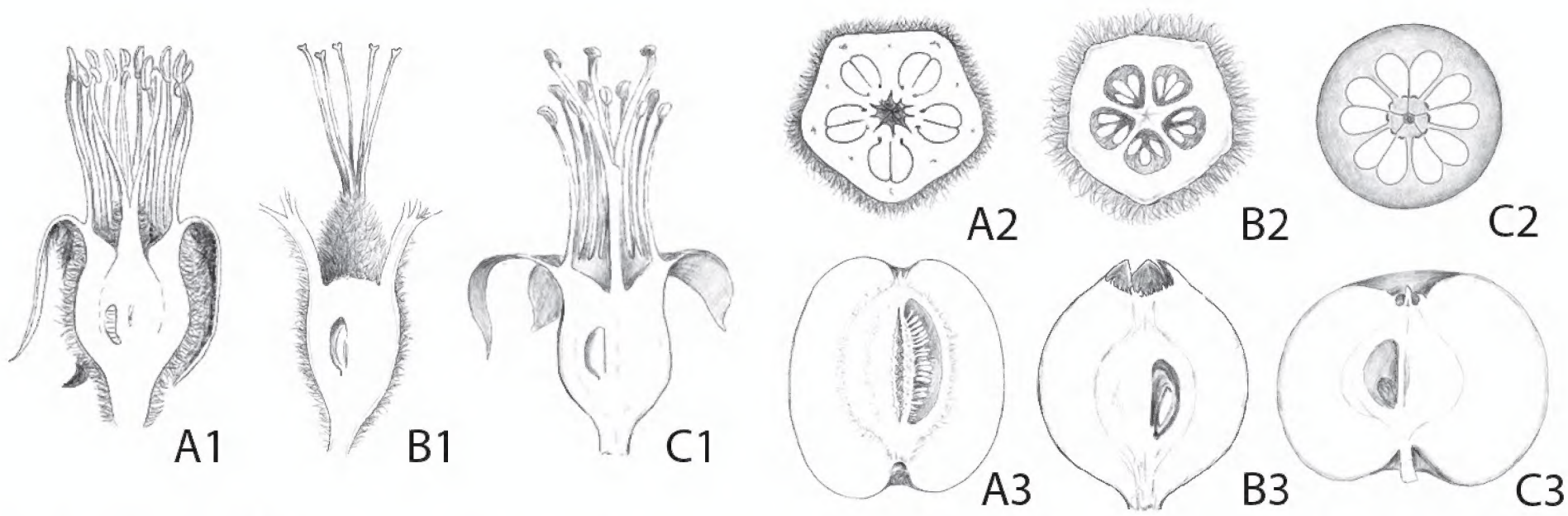

Figure 1. Morphological comparison amongst *Cydonia* (A1-A3), *Docynia* (B1-B3) and *Malus* (C1-C3) **A1, B1, C1** longitudinal section of carpel **A2, B2, C2** cross-section of fruit **A3, B3, C3** longitudinal section of fruit.

al. 2019, 2020a, 2020b, 2022; Jin et al. 2023). Several shared morphological characteristics have also supported their close relationship, i.e. cone-shaped non-adnate part of the ovaries (Fig. 1B1, C1), fully connate carpels (Fig. 1B1, C1), incurved and persistent calyx, numerous scattered sclereids throughout the flesh, juvenile leaves deeply lobed and similar flavonoid chemistry (Williams 1982; Robertson et al. 1991; Kalkman 2004). However, Jin (2014) proposed an alternative phylogenetic inference, based on the whole plastome, the sister relationship between *Docynia* and *Cydonia*. Additionally, Xiang et al. (2017) inferred a close relationship between *Docynia* and *Eriolobus* M.Roem., based on the transcriptomic data and this result provided another line of evidence for Schneider's (1906) taxonomic transfer. However, Xiang et al. (2017) sampled only four apple-related species, *Malus baccata* (L.) Borkh., *M. domestica* (Suckow) Borkh., *Docynia delavayi* (Franch.) C.K.Schneid. and *Eriolobus trilobatus* M.Roem., the inferred phylogenomic topology based on this limited taxon sampling; thus, an accurate species relationship was not presented. Therefore, the argument that *Docynia* should be transferred to the genus *Eriolobus*, based on a strongly-supported sister relationship between the two taxa is untenable, as this evidence with limited taxon sampling is insufficient to justify a taxonomic reclassification proposed by Schneider (1906). Liu et al. (2022) sampled 39 individuals representing 18 wild species and provided a robust backbone of the apple and its allies in the framework of the tribe Maleae integrating 797 single-copy nuclear genes (SCN genes) and whole plastome data (Fig. 2). This phylogenomic analyses resolved the phylogenetic position of *Docynia*, placing it within *Malus* sensu lato (Liu et al. 2022).

In this study, we aim to transfer three currently-recognised species of *Docynia* to *Malus*.

Materials and methods

We sampled 77 individuals in the framework of Maleae, of which 39 were apple-related species and the other 38 were outgroup species. All these 77 samples were performed for deep genome skimming (DGS) sequencing with 5-10G data for each sample. We assembled the whole plastome using NOVOPlasty v. 4.3.1 (Dierckxsens et al. 2016) and a successive assembly approach (Liu et al. 2021).

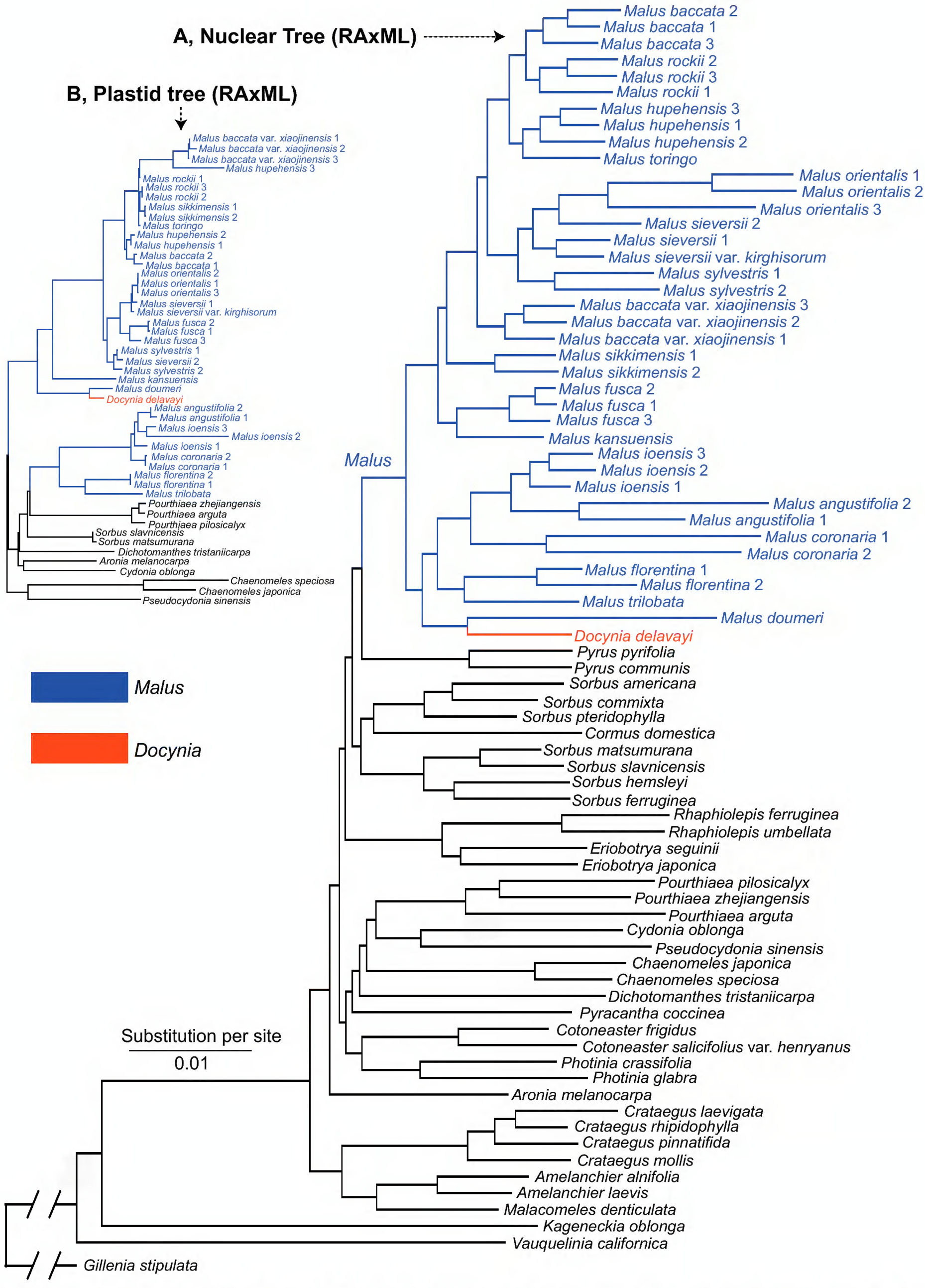

Figure 2. Maximum Likelihood (ML) tree of *Malus* within Maleae inferred from RAxML analysis using the concatenated 797 single-copy nuclear genes (SCNs) supermatrix (A), the upper left inset is a portion of the RAxML tree of *Malus*, based on the 78 concatenated plastid coding sequences (CDSs) supermatrix. (Adapted from figs 2 & 5 in Liu et al. (2022)).

Given the rich genomic resources in various lineages of Rosaceae, we screened 797 nuclear SCN genes from six genomes, *Malus baccata*, *M. domestica*, *Pyrus betulifolia* Bunge, *P. bretschneideri* Rehder, *P. ussuriensis* Maxim. × *P. communis* L. and *P. pyrifolia* (Burm.f.) Nakai. We assembled these 797 nuclear SCN genes for these 77 samples using HybPiper pipeline v. 1.3.1 (Johnson et al. 2016). The assembled sequences were then cleaned with a series of procedures, such as trimAL v. 1.2 (Capella-Gutiérrez et al. 2009), AMAS v. 1.0 (Borowiec 2016), TreeShrink v. 1.3.9 (Mai and Mirarab 2018) and Spruceup (Borowiec 2019). We combined the concatenated and coalescent-based methods for accurate phylogenetic inference. As for the concatenated-based method, we performed Maximum Likelihood (ML) tree inference using RAxML 8.2.12 (Stamatakis 2014) and IQ-TREE2 v. 2.1.3 (Minh et al. 2020). The shrunken trees from TreeShrink (Mai and Mirarab 2018) were used as input to estimate a coalescent-based species tree with ASTRAL-III (Zhang et al. 2018). The detailed parameters refer to the materials and methods in Liu et al. (2022).

Results and discussion

The phylogenetic relationship between *Docynia* and *Malus* has been controversial for two centuries. Our results revealed that all these nine nuclear and plastid trees in our study (Liu et al. 2022) demonstrated the paraphyly of *Malus* s.s., with *Docynia* nested within it (Fig. 2) and this was also confirmed in several recent molecular studies (Lo and Donoghue 2012; Xiang et al. 2017; Liu et al. 2020a). The sister relationship between *Docynia* and *Malus doumeri* A.Chev. (= *Docyniopsis*) was confirmed either in the nuclear or plastid trees, except for the conflicting phylogenetic placement of the *Docynia-Docyniopsis* clade. As indicated in our previous study (Liu et al. 2022), the close relationship between *Docynia* and *Docyniopsis* (Fig. 3) was also supported by the morphological evidence, such as cone-shaped non-adnate part of the ovaries (Figs 1B1, C1, 3I), fully connate carpels (Figs 1B1, C1, 3K), incurved and persistent calyx (Fig. 3A, F, I, J), numerous scattered sclereids throughout the flesh, juvenile leaves deeply lobed and similar flavonoid chemistry (Williams 1982; Robertson et al. 1991; Kalkman 2004).

Despite the monophyly of narrowly-circumscribed small genera in *Malus* s.l., including *Chloromeles* (Decne.) Decne., *Docynia*, *Docyniopsis*, *Eriolobus* M.Roem. and *Malus* sensu stricto, we believe that such narrow generic concepts may be impractical for use by botanists, ecologists, conservation biologists and horticulturalists. Given the prevalence of reticulations in angiosperms, we recommend integrating multiple lines of evidence for accurate taxonomic treatments, including morphology, phylogenomics, cytology, biogeography and ecology, as proposed by integrative systematics (Wen et al. 2017). Traditionally, taxonomic circumscription was often focused solely on the taxonomic community, with little consideration given to its broader implications. However, today there is a growing recognition that taxonomic circumscription can have far-reaching effects on many aspects of biology, including conservation, ecology and evolution. By considering the needs of the broader biological community, taxonomic circumscription can help to ensure that taxonomic classifications are more valuable and relevant to a wider range of researchers and practitioners. An excessive inclination towards separating genera can hinder

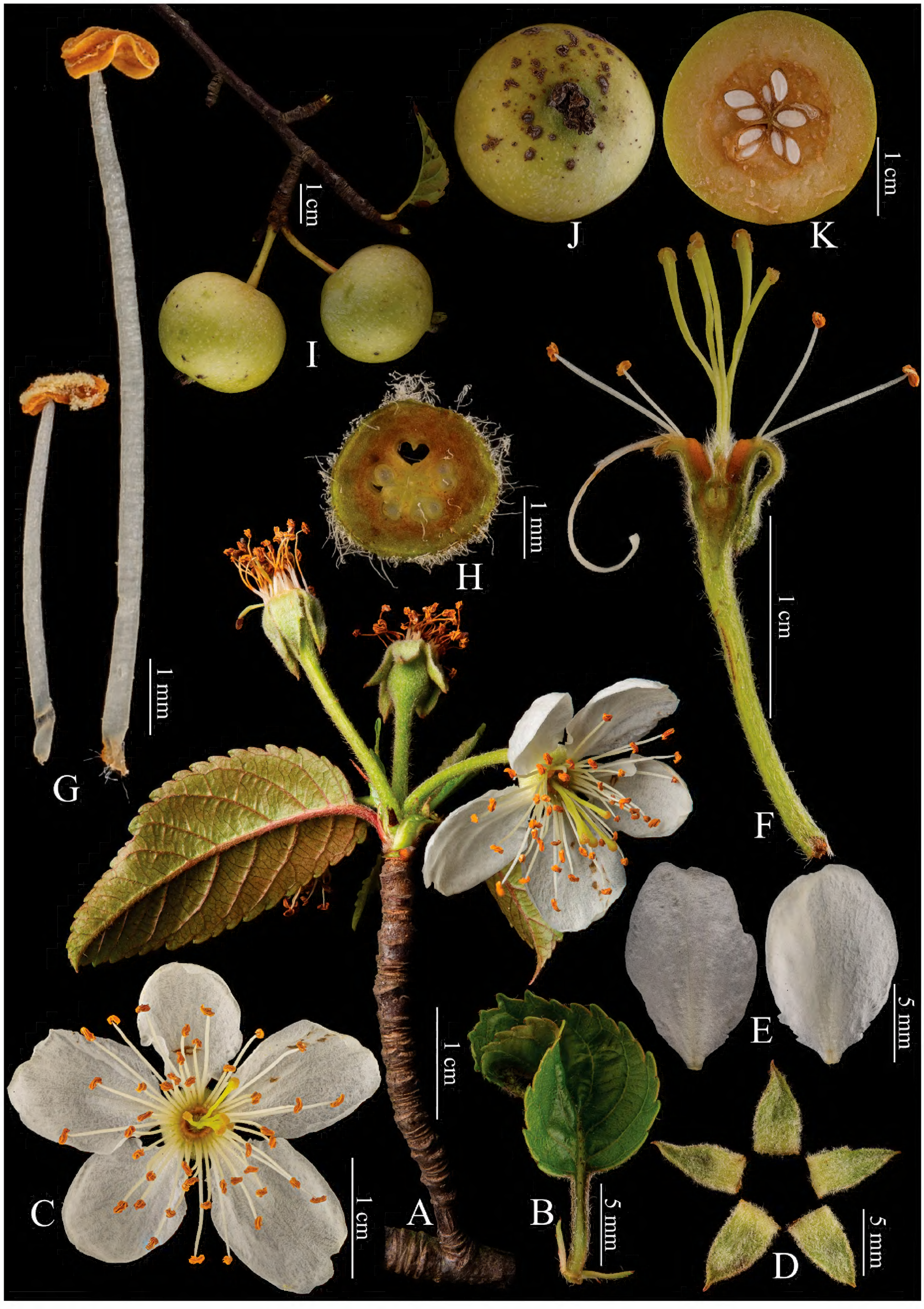

Figure 3. Structural comparison of the represented species in *Malus* sect. *Docyniopsis*, *M. doumeri* **A** inflorescence branch with young fruits **B** undeveloped leaves **C** flower **D** sepals (five) **E** petals **F** longitudinal section of flower **G** filament **H, K** cross-section of fruit in different stages **I** infructescence branch **J** the projected pome at apex and the persistent sepals. All photos credit to Bin-Jie Ge.

the advancement of research programmes for understanding evolution across all descendants stemming from a common ancestor. Additionally, by educating the general public about the importance of taxonomic circumscription, we can help foster a greater appreciation for biodiversity and its role in understanding and conserving it. In summary, taxonomic circumscription today should be viewed as a tool for serving the needs of both the taxonomic community and the broader biological community, as well as educating the general public about the importance of biodiversity and taxonomy (Wen et al. 2015, 2017; Funk 2018).

With all these considerations, we propose using the broad generic concept of *Malus*, which includes all members of *Malus* sensu Gu and Spongberg (2003) and the species in *Docynia*. We here formally transferred the three currently-recognised species of *Docynia* to *Malus* in the following text.

Taxonomic treatment

Malus indica **(Wall.) B.B.Liu, comb. nov.**

urn:lsid:ipni.org:names:77322788-1

Figs 4, 5

Chinese name: 多依; pinyin (spelled as it sounds): duo yi

≡ *Pyrus indica* Wall., Pl. Asiat. Rar. (Wallich) 2(8): 56 (1831). Type: Tab. 173 (holotype, Fig. 4). INDIA. "Khasia reg. temp. alt. 6000 pds", *J.D. Hooker & T. Thomson 510* (**epitype, designated here**: M [barcode M0213698]!). Note 1. Image of the epitype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.m0213698.

≡ *Cydonia indica* (Wall.) Spach, Hist. Nat. Vég. (Spach) 2: 158 (1834). Type: Based on *Pyrus indica* Wall.

≡ *Docynia indica* (Wall.) Decne., Nouv. Arch. Mus. Hist. Nat. 10: 131 (1874). Type: Based on *Pyrus indica* Wall.

≡ *Eriolobus indica* (Wall.) C.K.Schneid., Ill. Handb. Laubholzk. 1: 728 (1906). Type: Based on *Pyrus indica* Wall.

= *Docynia griffithiana* Decne., Nouv. Arch. Mus. Par. 10: 131 (1874). Type: INDIA. "Himalaya oriental.", *Griffith 2082* (holotype: P [barcode P01819345]!; isotypes: E [barcode E00010836]!, K, CAL [accession no. 153563]). Image of the holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p01819345.

= *Docynia indica* var. *griffithiana* (Decne.) Ghora, Bull. Bot. Surv. India 47(1–4): 150 (2005). Type: Based on *Docynia griffithiana* Decne.

= *Docynia hookeriana* Decne., Nouv. Arch. Mus. Par. 10: 131 (1874). Type: INDIA. "Khasia, regio temp. alt. 5000 pds.", *J.D. Hooker & T. Thomson 511* (holotype: P [barcode P01819346]!). Image of the holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p01819346.

= *Pyrus rufifolia* H.Lév., Bull. Géogr. Bot. 25: 46 (1915), [*Pirus*]. Type: CHINA. Yunnan: "flane des coteaux arides à Lou-Pou, 3050 m, Juin 1912", *E.E. Maire s.n.* (holotype: E [barcode E00010835]!). Image of the holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00010835.

= *Docynia rufifolia* (H.Lév.) Rehder, J. Arnold Arbor. 13: 310 (1932). Type: Based on *Pyrus rufifolia* H.Lév.

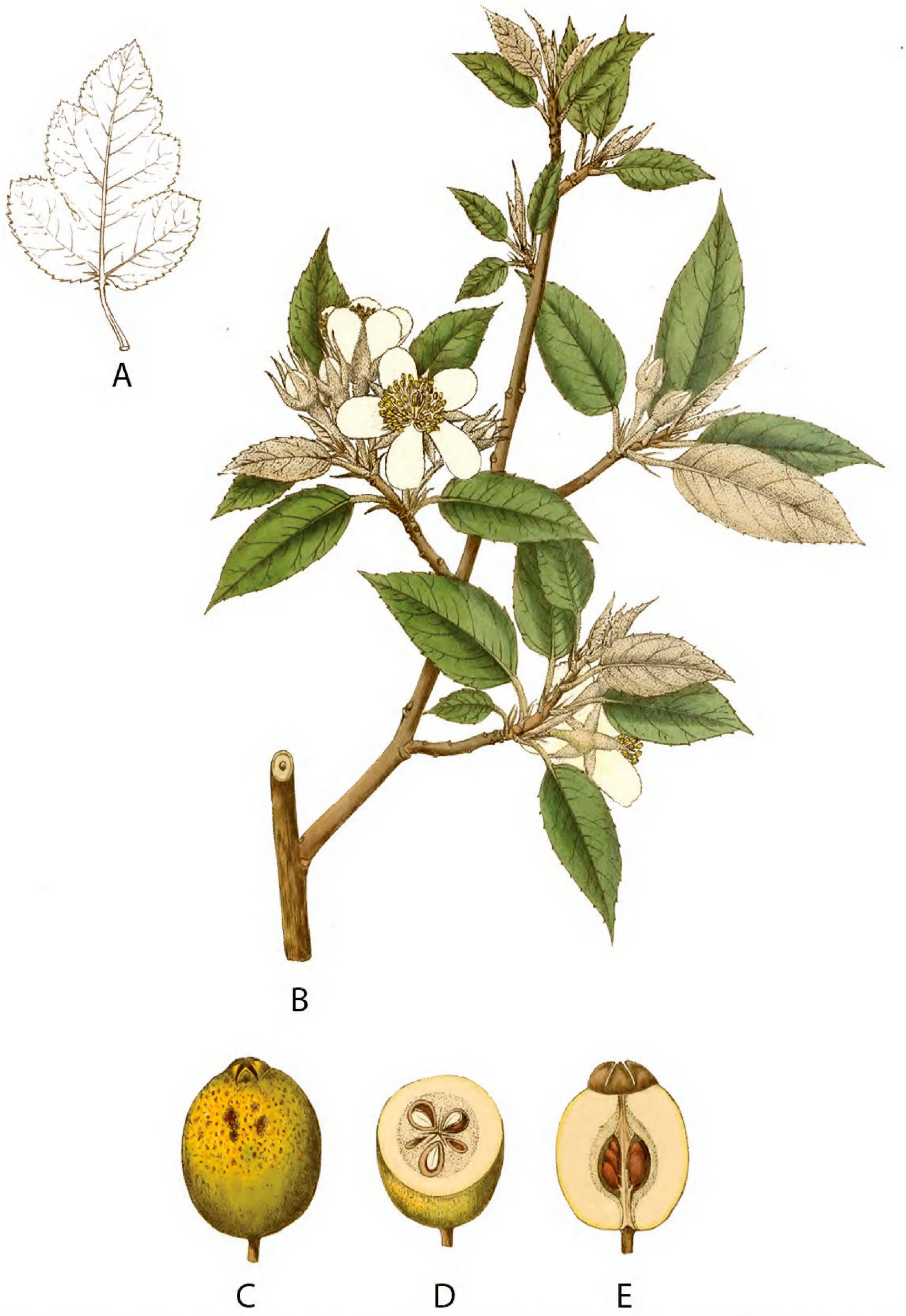

Figure 4. Holotype of *Malus indica* (redrawn from the illustration of Pl. Asiat. Rar. (Wallich 1831). 2: t. 173, 1831) **A** lobed-leaf **B** inflorescence branch **C** fruit **D** cross-section of fruit **E** longitudinal section of fruit.

Figure 5. *Malus indica* (Wall.) B.B.Liu **A** young fruit **B** fruit (cross-section) **C** fruit (longitudinal section) **D** flower **E** leaf branch **F** overview of tree. Photo credits: **A, B, D, E** and **F** to Jian Huang; **C** to Bin-Jie Ge.

= *Malus docynioides* C.K.Schneid., Bot. Gaz. 63: 400 (1917). Type: CHINA. Sichuan: "Szechuan australis: inter Kua-pie et Ta-tiao-ko, alt. ca. 2700 m, 23 Maji 1914", *C.K. Schneider 1349* (holotype: K [barcode K000758093]!; isotype: A [barcode 00026465]!). Image of the holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758093.

= *Docynia docynioides* (C.K.Schneid.) Rehder, J. Arnold Arbor. 2(1): 58 (1920). Type: Based on *Malus docynioides* C.K.Schneid.

Distribution. Bhutan, China (Sichuan and Yunnan), India, Myanmar, Nepal, Pakistan, Sikkim, Thailand and Vietnam.

Note 1. In the protologue of *Pyrus indica*, Wallich (1831) did not designate a specimen as the holotype, but only provided an illustration, which is considered to be the holotype (Fig. 4). However, the accurate identification of this species will be significantly impeded due to the limited morphological details in the illustration compared to the specimens (Turland et al. 2018). Consequently, it becomes necessary to select a single specimen as the epitype in order to distinguish it from its closest relatives, such as *Malus delavayi* and *M. longiunguis*. Decaisne (1874) cited two specimens (*J.D. Hooker & T. Thomson 509* and *J.D. Hooker & T. Thomson 510*) while transferring this species to *Docynia* as *Docynia indica*. Therefore, herein, we select a well-preserved specimen in the herbarium M (*J.D. Hooker & T. Thomson 510*: M0213698) as the epitype.

***Malus delavayi* (Franch.) B.B.Liu, comb. nov.**

urn:lsid:ipni.org:names:77322789-1

Fig. 6

Chinese name: 云南多依; pinyin (spelled as it sounds): yun nan duo yi

≡ *Pyrus delavayi* Franch., Pl. Delavay.: 227, t. 47 (1890), [*Pirus*]. Type: CHINA. Yunnan: "in montibus calcareis ad Mao-kou-tchang, supra Tapin-tze, prope Tali, alt. 2200 m.", 14 April 1884, *P.J.M. Delavay 466* (**lectotype, designated here**: P [barcode P01819347]!; isolectotype: L [barcode L0019412]!); ibidem, *P.J.M. Delavay 890* (syntype: K [barcode K000758091]!); in silvis ad orientem versus montis Hee-chan-tong, alt. 2500 m, 5 April 1887 (syntypes: K [barcode K000758090]!, K [barcode K000758092]!). Image of the lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p01819347.

≡ *Eriolobus delavayi* (Franch.) C.K.Schneid., Ill. Handb. Laubholzk. 1: 727 (1906). Type: Based on *Pyrus delavayi* Franch.

≡ *Docynia delavayi* (Franch.) C.K.Schneid., Repert. Spec. Nov. Regni Veg. 3: 180 (1906). Type: Based on *Pyrus delavayi* Franch.

≡ *Cydonia delavayi* (Franch.) Cardot, Bull. Mus. Natl. Hist. Nat. 24: 63 (1918). Type: Based on *Pyrus delavayi* Franch.

= *Cotoneaster bodinieri* H.Lév., Bull. Géogr. Bot. 25: 44 (1915). Type: CHINA. Yunnan: "montagnes près de la frontière du Kouy-Tchéou; à Kiang-Ty", 9 April 1897, *G. Bodinier s.n.* (holotype: E [barcode E00010834]!; isotype: A [barcode 00026464]!). Image of the holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00010834.

Distribution. China (Guizhou, Sichuan, and Yunnan).

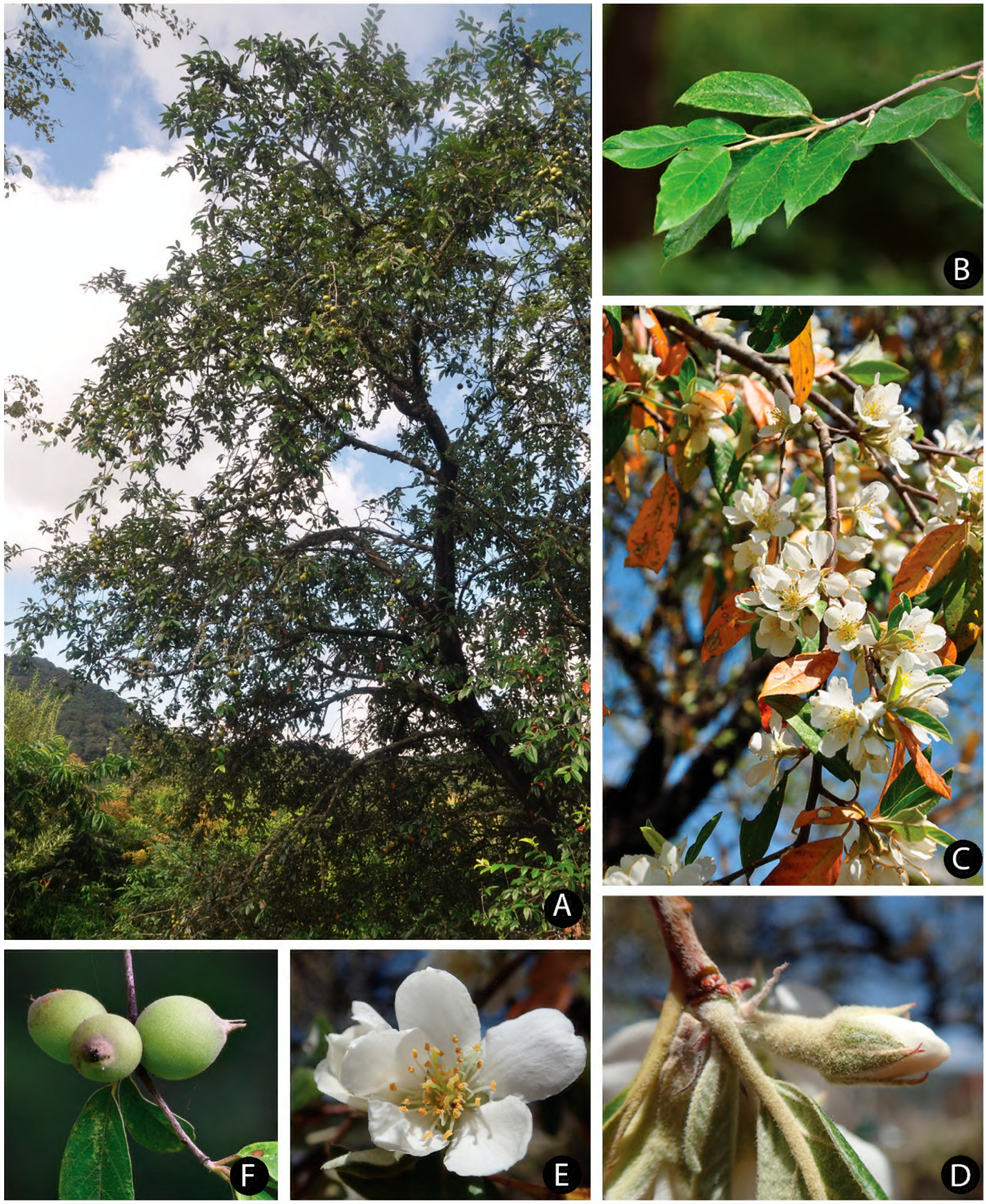

Figure 6. *Malus delavayi* (Franch.) B.B.Liu **A** overview of tree **B** leaf branch **C** inflorescence branch **D** flower buds **E** flower **F** young fruits. Photo credits to Jian Huang.

Figure 7. *Malus longiunguis* (Q.Luo & J.L.Liu) B.B.Liu **A** fruit branch **B** flower **C** young fruit. Photos credit to Qiang Luo.

Malus longiunguis **(Q.Luo & J.L.Liu) B.B.Liu, comb. nov.**
urn:lsid:ipni.org:names:77322790-1
Fig. 7
Chinese name: 长爪多依; pinyin (spelled as it sounds): chang zhua duo yi

≡ *Docynia longiunguis* Q.Luo & J.L.Liu, Bull. Bot. Res., Harbin 31(4): 389 (2011). Type: CHINA. Sichuan: Xichang, Lushan, alt. 1860 m, 18 March 2010, *Q. Luo 010304* (holotype: PE [barcode 02362758]!). Note 2.

Distribution. China (Sichuan).

Note 2. In the protologue, the holotype is indicated as being deposited in the herbarium of Xichang College (HXCH, Luo et al. 2011); however, this holotype specimen was then sent to the China National Herbarium (PE).

Acknowledgements

We thank Bing Liu (PE) for his careful review on the taxonomic transfer.

Additional information

Conflict of interest

No conflict of interest was declared.

Ethical statement

No ethical statement was reported.

Funding

National Natural Science Foundation of China (grant number 32000163 to BBL and 32270216 to BBL), the Youth Innovation Promotion Association CAS (grant number 2023086 to BBL), Shanghai Municipal Administration of Forestation and City Appearances (grant number G212416), and the Project of National Plant Specimen Resource Center (NPSRC) (grant number E0117G1001).

Author contributions

G.N.L designed and led the project. B.B.L and Y.W supervised the study. G.N.L, D.K.M, and C.X drafted the manuscript. J.H, B.J.G, and Q.L provided the photos in this paper. All the authors approved the final manuscript.

Author ORCIDs

Guang-Ning Liu https://orcid.org/0009-0009-0765-0392
Dai-Kun Ma https://orcid.org/0009-0005-5523-508X
Chao Xu https://orcid.org/0000-0002-9678-4772
Jian Huang https://orcid.org/0000-0002-2253-4586
Bin-Jie Ge https://orcid.org/0000-0002-4232-3567
Qiang Luo https://orcid.org/0000-0001-5043-2539
Yu Wei https://orcid.org/0000-0002-2013-4829
Bin-Bin Liu https://orcid.org/0000-0002-0297-7531

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

References

Borowiec ML (2016) AMAS: A fast tool for alignment manipulation and computing of summary statistics. PeerJ 4: e1660. https://doi.org/10.7717/peerj.1660

Borowiec ML (2019) Spruceup: Fast and flexible identification, visualization, and removal of outliers from large multiple sequence alignments. Journal of Open Source Software 4(42): 1635. https://doi.org/10.21105/joss.01635

Capella-Gutiérrez S, Silla-Martínez JM, Gabaldón T (2009) trimAl: A tool for automated alignment trimming in large-scale phylogenetic analyses. Bioinformatics (Oxford, England) 25(15): 1972–1973. https://doi.org/10.1093/bioinformatics/btp348

Decaisne MJ (1874) Mémoire sur la Famille des Pomacées. Archives du Muséum d`Histoire Naturelle, Paris 10: 45–192.

Dierckxsens N, Mardulyn P, Smits G (2016) Novoplasty: De novo assembly of organelle genomes from whole genome data. Nucleic Acids Research 45: e18. https://doi.org/10.1093/nar/gkw955

Focke WO (1888) Rosaceae. In: Engler A, Krause K, Pilger RKF, Prantl K (Eds) Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten, insbesondere den Nutzpflanzen, unter Mitwirkung zahlreicher hervorragender Fachgelehrten begründet, T. 3, Abt. 3. Verlag von Wilhelm Engelmann, Leipzig, 1–61.

Funk VA (2018) Collections-based science in the 21st century. Journal of Systematics and Evolution 56(3): 175–193. https://doi.org/10.1111/jse.12315

Gu CZ, Spongberg SA (2003) Rosaceae. In: Wu ZY, Raven PH, Hong DY (Eds) Flora of China (Vol. 9) Pittosporaceae through Connaraceae. Science Press, Beijing & Missouri Botanical Garden Press, St. Louis, 46–434.

Jin GH (2014) Phylogenomics and biogeography of *Malus* Mill. M.D Thesis, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming. [In Chinese]

Jin ZT, Hodel RGJ, Ma DK, Wang H, Liu GN, Ren C, Ge BJ, Fan Q, Jin SH, Xu C, Wu J, Liu BB (2023) Nightmare or delight: taxonomic circumscription meets reticulate evolution in the phylogenomic era. bioRxiv, 1–68. https://doi.org/10.1101/2023.03.28.534649

Johnson MG, Gardner EM, Liu Y, Medina R, Goffinet B, Shaw AJ, Zerega NJC, Wickett NJ (2016) HybPiper: Extracting coding sequence and introns for phylogenetics from high-throughput sequencing reads using target enrichment. Applications in Plant Sciences 4(7): 1600016. https://doi.org/10.3732/apps.1600016

Kalkman C (2004) Rosaceae. In: Kubitzki K (Ed.) The Families and Genera of Vascular Plants. Springer, Berlin, 138–141. https://doi.org/10.1007/978-3-662-07257-8_39

Koehne BAE (1893) Deutsche Dendrologie. Verlag von Ferdinand Enke, Stuttgart. [In German]

Liu BB, Hong DY, Zhou SL, Xu C, Dong WP, Johnson G, Wen J (2019) Phylogenomic analyses of the *Photinia* complex support the recognition of a new genus *Phippsiomeles* and the resurrection of a redefined *Stranvaesia* in Maleae (Rosaceae). Journal of Systematics and Evolution 57(6): 678–694. https://doi.org/10.1111/jse.12542

Liu BB, Campbell CS, Hong DY, Wen J (2020a) Phylogenetic relationships and chloroplast capture in the *Amelanchier-Malacomeles-Peraphyllum* clade (Maleae, Rosaceae): Evidence from chloroplast genome and nuclear ribosomal DNA data using genome skimming. Molecular Phylogenetics and Evolution 147: 106784. https://doi.org/10.1016/j.ympev.2020.106784

Liu BB, Liu GN, Hong DY, Wen J (2020b) *Eriobotrya* belongs to *Rhaphiolepis* (Maleae, Rosaceae): Evidence from chloroplast genome and nuclear ribosomal DNA data. Frontiers in Plant Science 10: e1731. https://doi.org/10.3389/fpls.2019.01731

Liu BB, Ma ZY, Ren C, Hodel RGJ, Sun M, Liu XQ, Liu GN, Hong DY, Zimmer EA, Wen J (2021) Capturing single-copy nuclear genes, organellar genomes, and nuclear ribosomal DNA from deep genome skimming data for plant phylogenetics: A case study in Vitaceae. Journal of Systematics and Evolution 59(5): 1124–1138. https://doi.org/10.1111/jse.12806

Liu BB, Ren C, Kwak M, Hodel RGJ, Xu C, He J, Zhou WB, Huang CH, Ma H, Qian GZ, Hong DY, Wen J (2022) Phylogenomic conflict analyses in the apple genus *Malus* s.l. reveal widespread hybridization and allopolyploidy driving diversification, with insights into the complex biogeographic history in the Northern Hemisphere. Journal of Integrative Plant Biology 64(5): 1020–1043. https://doi.org/10.1111/jipb.13246

Lo EYY, Donoghue MJ (2012) Expanded phylogenetic and dating analyses of the apples and their relatives (Pyreae, Rosaceae). Molecular Phylogenetics and Evolution 63(2): 230–243. https://doi.org/10.1016/j.ympev.2011.10.005

Luo Q, Liu JL, Cai GZ (2011) *Docynia longiunguis* Q.Luo et J.L.Liu, a new species of *Docynia* Dcne. from China. Bulletin of Botanical Research 31: 389–391. https://doi.org/10.7525/j.issn.1673-5102.2011.04.002

Mai U, Mirarab S (2018) TreeShrink: Fast and accurate detection of outlier long branches in collections of phylogenetic trees. BMC Genomics 19(S5): 272. https://doi.org/10.1186/s12864-018-4620-2

Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, Von Haeseler A, Lanfear R (2020) IQ-TREE 2: New models and efficient methods for phylogenetic

inference in the genomic era. Molecular Biology and Evolution 37(5): 1530–1534. https://doi.org/10.1093/molbev/msaa015

Phipps JB, Robertson KR, Smith PG, Rohrer JR (1990) A checklist of the subfamily Maloideae (Rosaceae). Canadian Journal of Botany 68(10): 2209–2269. https://doi.org/10.1139/b90-288

Rehder A (1940) Manual of cultivated trees and shrubs hardy in North America, exclusive of the subtropical and warmer temperate regions, 2nd edn. The Macmillan Company, New York, 876 pp.

Rehder A (1949) Bibliography of cultivated trees and shrubs hardy in the cooler temperate regions of the Northern Hemisphere. The Arnold Arboretum of Harvard University, Jamaica Plain, Massachusetts.

Robertson KR, Phipps JB, Rohrer JR, Smith PG (1991) A synopsis of genera in Maloideae (Rosaceae). Systematic Botany 16(2): 376–394. https://doi.org/10.2307/2419287

Schneider CK (1906) Illustriertes Handbuch der Laubholzkunde. Verlag von Gustav Fisher, Jena.

Spach E (1834) Histoire Naturelle des Végétaux. Phanerogames, vol. 2. Librairie encyclopédique de Roret, Paris, 510 pp.

Stamatakis A (2014) RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics (Oxford, England) 30(9): 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth D, Herendeen PS, Knapp S, Kusber WH, Li DZ, Marhold K (2018) International code of nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Koeltz Botanical Books, Glashütten. https://doi.org/10.12705/Code.2018

Wallich N (1831) Plantae Asiaticae Rariores: or, descriptions and figures of a select number of unpublished East Indian plants, vol. 2. Treuttel and Würtz, London, 56 pp. https://doi.org/10.5962/bhl.title.468

Wen J, Ickert-Bond SM, Appelhans MS, Dorr LJ, Funk VA (2015) Collections-based systematics: Opportunities and outlook for 2050. Journal of Systematics and Evolution 53(6): 477–488. https://doi.org/10.1111/jse.12181

Wen J, Harris AJ, Ickert-Bond SM, Dikow R, Wurdack K, Zimmer EA (2017) Developing integrative systematics in the informatics and genomic era, and calling for a global Biodiversity Cyberbank. Journal of Systematics and Evolution 55(4): 308–321. https://doi.org/10.1111/jse.12270

Wenzig T (1883) Die Pomaceen. Charaktere der Gattungen und Arten. Jahrbuch des Königlichen Botanischen Gartens und des Botanischen Museums zu Berlin 2: 287–307.

Williams AH (1982) Chemical evidence from the flavonoids relevant to the classification of *Malus* species. Botanical Journal of the Linnean Society 84(1): 31–39. https://doi.org/10.1111/j.1095-8339.1982.tb00358.x

Xiang YZ, Huang C-H, Hu Y, Wen J, Li SS, Yi TS, Chen HY, Xiang J, Ma H (2017) Evolution of Rosaceae fruit types based on nuclear phylogeny in the context of geological times and genome duplication. Molecular Biology and Evolution 34: 262–281. https://doi.org/10.1093/molbev/msw242

Yu TT, Ku TC (1974) *Docynia* Dcne., *Malus* Mill. In: Yu TT (Ed.) Flora Reipublicae Popularis Sinicae, Tomus 36. Science Press, Beijing, 345–348, 372–402.

Zhang C, Rabiee M, Sayyari E, Mirarab S (2018) ASTRAL-III: Polynomial time species tree reconstruction from partially resolved gene trees. BMC Bioinformatics 19(S6): 153. https://doi.org/10.1186/s12859-018-2129-y